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Motion in the ocean – paradigm shift in movement ecology requires "sedentary" organisms to be redefined

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Abstract

In Focus: Hamel J-F, Sun J, Gianasi BL, et al. (2019). Active buoyancy adjustment increases dispersal potential in benthic marine animals. Journal of Animal Ecology, 00:1–13. https://doi.org/10.1111/1365-2656.12943

Effective ecosystem-based fisheries and conservation management relies on the accuracy of population structure and connectivity models. The majority of sedentary marine species are pelago-benthic, meaning the pelagic larval stages disperse using ocean currents, and the adults are stationary or crawl slowly over the seabed. Adult movement was, until recently, thought to be insignificant due to the limited spatial range. In this issue, a novel method of translocation for adults that may far exceed the dispersion capability of the juveniles is presented, providing evidence for important effects of adult dispersal. Active Buoyancy Adjustment (ABA) is a behavioural response to environmental stressors or water currents, that enables echinoderm Asteroidea (sea stars) and Holothuroidea (sea cucumbers) to efficiently relocate. Adult relocation using tides could explain mass spawning aggregations that increase population and individual fitness, and less advantageous mass stranding events. Implications of ABA for future marine management and policy are discussed.

Movement is fundamental to ecological and evolutionary processes (Nathan et al., 2008). Dispersal patterns of organisms underpin management and conservation strategies (Allen & Singh, 2016). For marine organisms with pelago-benthic life histories, it continues to be accepted that pelagic larval dispersal in early life is the main driver responsible for shaping geographic distributions of populations (Allen, Metaxas, & Snelgrove, 2018), compared to the less influential slow directed movement associated with the sedentary adults (Castilla & Crisp, 1970; Nathan et al., 2008). In this issue, Hamel *et al.* (2019) present evidence that may cause a shift in pelago-benthic dispersal paradigms. Laboratory and field studies demonstrate an overlooked means of locomotion, "Active Buoyancy Adjustment" (ABA), in post-settlement benthic members of the echinoderm class Holothuroidea. ABA allows individuals to actively modify their buoyancy in order to detach from the seabed and relatively quickly relocate (move) using water currents.

The first anecdotal, published, field observation of ABA behaviour was documented off the south coast of England, where sea stars *Asterias rubens* were observed "starballing", i.e. bouncing along the seabed (Sheehan & Cousens, 2017). Video of the behaviour was recorded during a study to compare the efficacy of different towed underwater cameras systems. The behaviour was evident in approximately 30% of observed individuals and only seen during strong tidal flow (~0.5 m s^{-1}) and turbid water at ~20 m depth. The lack of any previous accounts of this behaviour in the literature suggested it might be infrequent and could therefore explain the rare mass stranding events suffered by *A. rubens* and other sedentary species (Sheehan & Cousens, 2017). This new discovery, while embraced by popular science (Plass, 2018) and since supported by other anecdotal observations in south Wales (Dr Andy Woolmer *pers.comm.*), was skeptically received by expert audiences. However, Hamel *et al.* (2019) and Johnson *et al.* (2019) have now demonstrated the mechanisms underlying this behaviour and provided evidence of its occurrence in multiple species and geographic regions. Together these studies have demonstrated the mechanisms underlying the behaviour in multiple species and geographic regions. Furthermore, the likely frequency of this behaviour is greater than first predicted. Hamel *et al.* (2019) demonstrate that ABA occurs during high flow and turbid waters in laboratory conditions and, therefore, could occur frequently and predictably. Unsuitable conditions such as high turbidity and strong currents are typically avoided for SCUBA or camera underwater surveys, which could explain the previous lack of ABA observations and continued belief that sedentary organisms are limited to slow locomotion during the adult post-settlement phase (Allen et al., 2018).

Hamel *et al.* (2019) used both laboratory and field studies in Newfoundland and Madagascar to understand when this phenomenon occurs and the physiological mechanisms behind it. The study focused on two commercially valuable and well-studied species of Holothuroidea sea cucumbers representing different taxonomic orders, geographic ranges and reproductive strategies. At each location, video footage was used to analyze behaviour and displacement of *Cucumaria frondosa* in Newfoundland (NFL) (41-57 m depth) and Nova Scotia (NS) (220 -300 m depth) (East Canada), and *Holothuria scabra* in Madagascar (0.10 – 2.5 m depth). Movement of sea cucumbers by tumbling over the seafloor was observed at all three locations. Furthermore, floating of sea cucumbers at the surface was observed at the site in Madagascar.

Field observations showed that for *C. frondosa*, 1.2-100% of the population samples were tumbling at speeds between 0.5 (NFL)- 0.83 (NS) m s^{-1} compared to conspecifics, which remained attached to the seabed. Individuals observed tumbling tended to be bloated with the ambulacral podia and tentacles retracted. *H. scabra* tended to exhibit ABA during the night, only during ebbing tides and were most frequent during full moons and the cool season.

Laboratory experiments showed that in the absence of stressors (turbidity, salinity, conspecific density) or water current both juvenile and adult *C. frondosa* remained attached to the substrate. At 6 months old, juveniles developed the ability to increase their body volume by 3.8 times. Individuals that did expand, did so in synchrony with all other expanding conspecifics, despite being housed separately. In the presence of stressors and/or currents the adults exhibited a range of behavioural changes, such as decreased strength of attachment to the substrate, retraction of tentacles, and bloating. The degree to which these behaviours were exerted depended on the severity of the stressor and speed of the current. Weak reactions were related to increases in conspecific density, while severe reactions were related to increases in salinity and turbidity. In the absence of stressors, the proportion of tumbling adults increased with increasing water current. Concurrent laboratory studies in the United States have also shown similar “bouncing” ability of three species of Asteroidea sea stars (*Protoreaster nodosus, Asterias forbesi and Luidia clathrata*) (Etzel et al., 2019). Comparisons were made regarding bounce and speed between different species’ size, ambulacral area from which podia (tube feet) emerge, and density of podia. The density and area of podia appeared less important than size and shape. *L. clathrata* that are relatively flat, bounced at higher frequencies and speeds than *P. nodosus* that are taller. Positive correlations between size, bounce frequency and speed were found for *P. nodosus* and *A. forbesi*, and the opposite was observed for *L. clathrate*.

ABA has been shown to occur in at least six echinoderm species so far where behavioural changes that cause detachment from the substrate have enabled tidally driven movement. The discovery of ABA behaviour could help elucidate unexplained observations, such as, mass strandings (Mcclintock, Mcclintock, & Lawrence, 2013) and mass subtidal aggregations (e.g. Sloan & Aldridge, 1981). While mass stranding events are fatal, mass subtidal aggregations could increase the fitness of these broadcast spawners. Greater densities of spawning adults increase the chances of reproductive success during spawning events (Pennington, 1985).

Echinoderms have diverse ecosystem roles, such as, scavengers, filter feeders, bioturbators, predators, prey and are targeted by commercial fisheries (Purcell, Conand, Uthicke, & Byrne, 2016). The implications for conservation, connectivity and movement ecology, which have so far underestimated their capacity for dispersal (Figure 1), are therefore, important to consider.

One approach to ecosystem-based fisheries and conservation management has been to develop networks of partially protected marine spaces that are representative of a range of species and habitats, working as a connected, functional unit (Moffitt, Wilson White, & Botsford, 2011). ABA has shown that the adult life stage of sedentary benthic species can have significantly greater locomotion than previously thought, with potential relevance to regional scale marine management. Therefore, predicted levels of connectivity based on larval dispersion may have underestimated how connected networks of MPA might be (Figure 1). The effect that storms might have on adult dispersal and stranding events is also worth considering, especially as storm frequency and magnitude is likely to increase with our changing climate (Zappa, Shaffrey, Hodges, Sansom, & Stephenson, 2013). To capture realistic estimates of metapopulation connectivity, adult-mediated dispersal should be factored in with traditional larval dispersal models (Frisk, Jordaan, & Miller, 2014). Regarding local scale management, as ABA occurs in benthic adults and is sensitive to stressors including water current and turbidity, to avoid disturbance, destructive activities that cause these responses, such as demersal towed fishing, could be directed away from coastal areas. If demersal towed fishing using nets or dredges does induce ABA, animals may escape capture or indeed be more prone to capture when bouncing, balling and tumbling over the seabed. ABA behaviour highlights that benthic species do not occupy small discrete areas and have the capacity to move within and between MPAs. To enable benthic systems to optimally function, the seabed requires appropriate management within and between MPAs. An ambitious start would be to exclude the most destructive fishing activities from MPAs, thereby adopting consistent management (the Whole Site Approach) rather than focused, feature specific management that allows demersal towed fishing within MPAs (Rees et al., 2013; Sheehan et al., 2013). While climate change remains a significant issue to be solved at a global level, local and regional management focused on removing persistent damaging activities in coastal areas could be effective in reducing disturbance that interrupts natural movement patterns of benthic organisms.

When ABA causes large numbers of spawning adults to aggregate, it is likely to increase the reproductive success and fitness of the population. However, if ABA results in mass stranding of organisms that often co-occur with extreme storm events, this could have deleterious effects on local populations. However, if stranded organisms are a result of ABA behaviour, individuals may not necessarily be diseased or damaged, and in the same way that beached whales and dolphins are re-immersed by volunteers, recently stranded invertebrates could also survive if returned to their marine realm.

In conclusion, ABA has the potential increase an organism's fitness by escaping predation, randomly and efficiently sourcing new foraging grounds, and aggregating spawning conspecifics. However, it is still unknown how extensive ABA is amongst echinoderms or other sedentary organisms. With more empirical and field based studies, such as Hamel *et al.*(2019), the nature and influence of dispersal at different life stages of benthic organisms can be revealed. These data are needed to inform and update benthic movement ecology theory, ecosystem fisheries and conservation management and policy. Modern advances in tracking technology using acoustic telemetry could provide important insights for movement ecology enabling ABA related displacement distances to be quantified and help redefine the term "sedentary".

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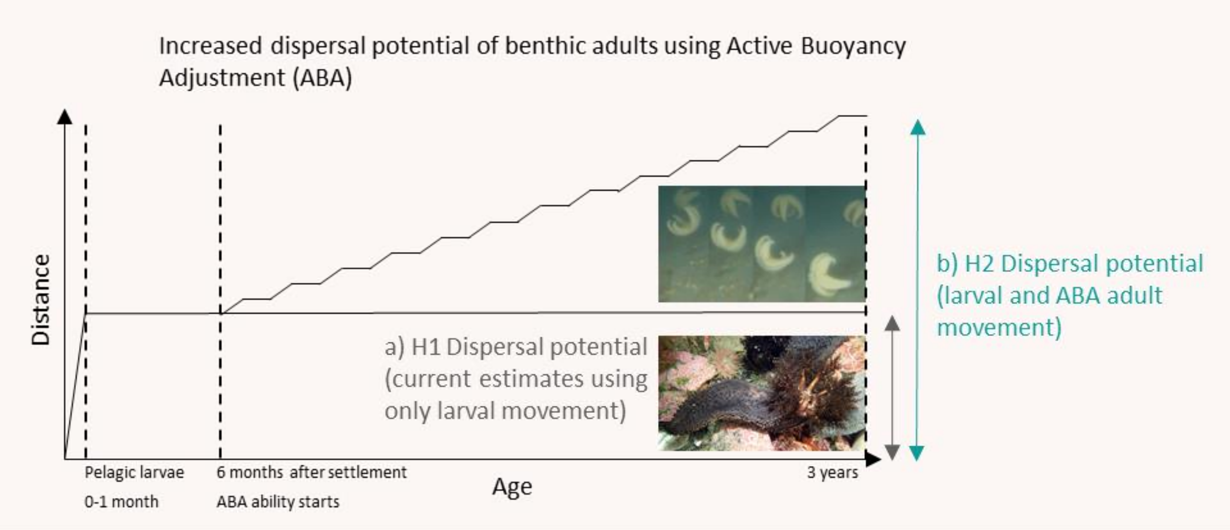

FIGURE 1 Active Buoyancy Adjustment (ABA) is a newly discovered behaviour that has been demonstrated in different echinoderm species and geographic regions (Hamel et al., 2019). It is a process where adults actively induce bloating, change their flesh to volume ratio, detach podia from the seabed and use water currents to facilitate efficient locomotion. Connectivity models for sedentary pelago-benthic organisms typically use only the larval phase to make dispersion predictions as adult locomotion was considered slow and insignificant (a) Hypothesis 1. The ABA model (b) Hypothesis 2 predicts that adult dispersion in sedentary organisms significantly exceeds the population dispersal predicted by current estimates. The schematic diagram shows a conservative depiction of the life-span of an echinoderm, with one month of pelagic larvae ending in settlement (first dotted line), ABA ability develops 6 months after settlement (second dotted line), the adult then intermittently switches between crawling benthic life, where feeding takes place, and balling, tumbling or bouncing using ABA to relocate, sometimes co-locating with conspecifics in mass spawning aggregations to increase fitness. The axis ends at three years old though echinoderms have the potential to live much longer and so predicted differences between hypotheses 1 & 2 could be greater than shown here.

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